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**A Cytotaxonomic Study
of the Genus Mnium**

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A CYTOTAXONOMIC STUDY OF THE GENUS *MNIUM**

ROBERT JAMES LOWRY

INTRODUCTION

The purpose of this investigation was to delimit the genus *Mnium* and to determine interspecific relationships of the North American species through an investigation of chromosome numbers and chromosome morphology.

That the present generic limits of the genus *Mnium* are not clearly understood by taxonomists is well illustrated by the uncertain position of *Mnium* (*Leucolepis*) *Menziesii*, *Mnium* (*Cinclidium*) *hymenophyllum*, *Mnium* (*Cinclidium*) *hymenophylloides*, and *Mnium* (*Trachycystis*) *flagellare*. Andrews (1940) includes *Mnium Menziesii* in the genus although acknowledging its independent position. Lindberg (1868) however, considered it of sufficient distinctiveness for generic rank and proposed the name *Leucolepis* for it. "*Mnium punctatum*" consists of a series of many puzzling forms and Loeske (1910) suggested that these forms be united with *Cinclidium*. Andrews agrees that its relationship is evidently closer to *Cinclidium* than to other *Mnium* species but he is unwilling to support a taxonomic union.

Several "species-pairs" whose members seem to be very closely related occur in *Mnium*. *Mnium affine* and *Mnium medium*, although readily separated by sex condition and cell size, are strikingly similar. *Mnium insigne* differs from *Mnium affine* only quantitatively and in the restricted geographic distribution of the former. Concerning these last two species, Andrews says that "*Mnium insigne* is obviously a derivative of the widely distributed and greatly varying *Mnium affine*." *Mnium marginatum* and *Mnium orthorhynchum*, separated by sex condition and cell size, agree in most other characters. *Mnium punctatum* presents a taxonomic problem. Several species and varieties have been recognized by many authors whereas others, and most recently Andrews, put all North American forms in one species.

With the above problems in mind and with the conviction that cytological data would be of aid in their solution and also because of its large number of easily available species, the genus *Mnium* was selected for this study.

As more data accumulate they demonstrate with increasing clarity that such cytological phenomena as polyploidy, hybridization, and gene mutation, coupled with isolation, are important factors contributing to the formation of new plant species and must be considered in any attempt to establish relationships within plant groups (Dobzhansky 1941). A review of the literature must therefore pay particular attention to those works which have contributed knowledge related to the above phenomena as they occur and affect the mosses.

* Paper from the Department of Botany of the University of Michigan, No. 853.



Pringsheim (1876), Stahl (1876), Brizi (1892), and Correns (1899) demonstrated that the gametophytic generation of mosses could be produced directly from the sporophytic generation by the development of protonemata from the somatic tissues of the seta and capsule. Pringsheim and Stahl, working independently, obtained regeneration of the setae of *Hypnum*, *Amblystegium*, *Bryum*, and *Ceratodon*. Brizi found that protonema may arise from the young capsule wall in *Funaria hygrometrica*. Correns was able to confirm the results of Pringsheim and Stahl with *Hypnum*, *Amblystegium*, *Bryum*, and *Ceratodon*, but obtained negative results with a number of other mosses.

The work of the Marchals (Élie & Émile Marchal 1906, 1907, 1909, 1911) clearly demonstrated that moss plants produced by regeneration of sporophytic tissues were actually diploid. The Marchals were primarily interested in the effect of apospory upon sex and found that doubling the chromosome number of a strictly dioicous moss, for example *Bryum caespiticium*, produced diploid gametophytes which were potentially bisexual and, in a fair number of instances, produced both antheridia and archegonia in the same perichaetium. They also reported a direct proportionality between the number of chromosomes and the volume of the nucleus and cell. This work definitely established the fact that polyploidy could occur in the mosses, at least experimentally, and demonstrated some of its effects upon the physiology and morphology of the plants, sex condition, nucleus and cell size. The Marchals suggested the possibility of sporophytic regeneration occurring in nature with the consequent formation of new polyploid forms. They mentioned in this connection a sterile, monoicous form of *Bryum atropurpureum* found by them in nature.

During the period from 1912 to 1923, cytological studies on the mosses were largely confined to gametogenesis and the developing androcyte of the antheridium was the favorite subject for observation. The only interest of these studies to the cytotaxonomist is that chromosome numbers were occasionally reported. Typical examples of studies of this kind appear among the works of Wilson (1908-1915), Allen (1912, 1917) and Woodburn (1915). Wilson contributed observations on nuclear division, spore formation, spermatogenesis, and sex condition. His results agree in essential features with those currently accepted for nuclear division and spore formation. However, his report of a body being "budded off" from the nucleolus in the spore mother cell during the metabolic stage preceding meiosis and persisting until synapsis has not been substantiated by subsequent observations of other workers. Wilson also attributed the origin of the blepharoplast, limosphere, and accessory body of the sperm to material derived from the nucleolus.

In 1915, Wilson reported the discovery of a bisexual gametophyte of *Mnium hornum* (a species which is considered to be dioicous) with six chromosomes and since this is the normal gametophytic number he concluded, contrary to the Marchals, that sex determination is not associated with meiosis, "but is brought about by metabolic processes which operate in the organism over a considerable part of its life history." Blakeslee's (1908) comment upon the

Marchals' work is interesting in this connection. He pointed out that a bisexual race of *Phycomyces nitens*, produced in essentially the same manner as the bisexual mosses of the Marchals, lost the bisexual character after more than a dozen vegetative generations and he felt that the Marchals were unjustified in concluding that their bisexual mosses could be maintained indefinitely by vegetative propagation.

Woodburn (1915) studied spermatogenesis in *Mnium affine* var. *ciliare* and found no evidence of polar bodies or plates. He did describe the appearance of the blepharoplast and "a vesicle enclosed within the coiled body of the sperm and containing cytoplasm and probably nuclear material" which disappeared as the sperm approached maturity.

In 1912, Allen assigned the nucleolar phenomena described by Wilson to inadequate fixation and in 1917 published a detailed account of spermatogenesis in *Polytrichum juniperinum*. He described irregular bodies, derived from plastid material, which formed broad plates at the poles of the spindle in the dividing spermatogenous tissue. These polar plates became gradually less extensive until at the last division previous to the formation of the sperms, a single body (centrosome) was present at the sharply focused poles of the spindle (Allen 1912). The limosphere was described as dividing unequally producing a small mass of material which became associated with the apical portion of the sperm nucleus and the remainder of the limosphere became associated with the posterior portion and gradually disappeared as the sperm assumed its mature form (Allen 1917).

In 1923, workers again turned their attention to aposporically produced polyploids. Schweizer (1923) produced aposporic 2N gametophytes of *Splachnum sphaericum* as well as triploid and tetraploid sporophytes by fertilizations involving N and 2N gametes and tetraploid gametophytes by regeneration of tetraploid sporophytes. He obtained results similar to those of the Marchals regarding apospory and its effect upon sexuality. The Marchals (1909), found that their aposporic diploids were for the most part sterile because of non-functional gametes. Diploid forms of *Splachnum sphaericum* obtained by Schweizer did produce sporophytes, however. Diploid gametophytes of *Bryum caespiticium* also occasionally produce sporophytes (Wettstein 1924a).

Bornhagen (1930) working with *Splachnum ampullaceum* and *Splachnum sphaericum* obtained results similar to those of Schweizer just reviewed and produced 2N and 4N gametophytes of the former species.

Arens (1940) determined the sex condition of members of the *Splachnaceae*, by means of single spore cultures. *Voitia nivalis*, *Tayloria serrata*, *Tayloria tenuis*, *Tayloria splachnoides*, *Froelichiana lingulata*, *Tetraplodon angustatus*, *Tetraplodon bryoides*, *Tetraplodon urceolatus*, *Splachnum ampullaceum*, and *Splachnum australe* were found to be "haplomonioicous." *Splachnum pedunculatum* (*sphaericum*), *Splachnum melanocaulon*, *Splachnum luteum*, *Splachnum rubrum*, and *Splachnum vasculosum* were found to be "haplodioicous."

In 1923, Wettstein began his famous studies on the morphology, physiology and development of mosses, with special reference to genetics. He obtained the first experimental evidence demonstrating that hybridization could occur in this plant group. Although supposedly natural hybrids had previously been described in taxonomic papers, Wettstein was the first to make actual crosses and analyze the progeny thereof. Working with members of the *Funariaceae*, he made the following successful crosses: *Funaria hygrometrica* $\times$ *Physcomitrium eurystomum* and its reciprocal; *Funaria hygrometrica* $\times$ *Physcomitrium pyriforme* and its reciprocal; *Funaria hygrometrica* $\times$ *Entosthodon fascicularis* and its reciprocal; *Funaria hygrometrica* $\times$ *Funaria mediterranea* and its reciprocal; *Physcomitrium eurystomum* $\times$ *Physcomitrium pyriforme* and its reciprocal; *Physcomitrella patens* $\times$ *Funaria hygrometrica*; *Physcomitrella patens* $\times$ *Physcomitrium pyriforme*; *Physcomitrella patens* $\times$ *Physcomitrium eurystomum* and its reciprocal. Hybrids between experimentally produced polyploid races were also obtained (Wettstein 1923, 1924a,b,c, 1928a).

Sporophytic characters are inherited in the same manner and exhibit the same types of hereditary phenomena as found in other 2N organisms. As would be expected, Wettstein found that gametophytic characters segregate in a 1:1 ratio. Dominance is not found to exist for gametophytic characters if the true haploid chromosome complement is present. In polyploid gametophytes, factors are at least duplicated and a condition suitable for the expression of dominance therefore exists. Dominance may be partial or complete, as in other organisms. From the predominance of maternal characters in gametophyte progeny resulting from interspecific and intergeneric crosses, Wettstein (1924b, 1926, 1928a, b) concluded that the cytoplasm, in addition to the chromosomes, is important genetically.

Wettstein carefully analyzed the effects of polyploidy upon morphological characters and found that doubling the chromosome number from haploid to diploid concomitantly roughly doubles the volume of the leaf cells. Doubling from 2N to 4N, however, increased cell volume in the ratio of 1:5.2. A comparison of N and 2N protonema cells demonstrated a ratio of volume of 1:1.96. Although chloroplast counts in N, 2N, and 4N leaf cells were found to be 14.4, 26, and 63.37 respectively, the size of the chloroplasts seemed unchanged. The total number of leaf cells in N, 2N, and 4N races was found to be approximately the same. Size (length and width) of antheridia, archegonia, leaves, and capsules showed an increase as the chromosome number was increased.

Wettstein (1924c) appears to have been the first to induce polyploidy in mosses by chemical treatment. By injecting young capsules of *Funaria hygrometrica* with .01 % chloral hydrate and also .1 % potassium nitrate, he obtained a few 2N spores. He also caused doubling of the chromosome number by treating protonema with a dilute chloral hydrate solution, ether, and chloroform vapor. Low temperature and centrifuging were also found to be effective in inhibiting cell division since they resulted in the production of diploid cells.

Heitz (1945) obtained polyploid gametophytes of *Aulacomnium androgynum* by treating propagula and protonema with colchicine.

Doubling the chromosome number of a dioicous moss through apospory results in a potentially bisexual race. The ratio of synoicous plants to plants which produce only antheridia or archegonia in recently-produced 2N races is variable. The usual condition seems to be a preponderance of plants which produce only antheridia (Marchal & Marchal 1907). Most 2N races of originally dioicous mosses are highly sterile, although occasionally sporophytes are produced (Wettstein 1924c; Schweizer 1923). The origin of a completely fertile 2N race of *Bryum caespitium* is very interesting with regard to its loss of sterility. When first produced the race was highly sterile and produced only antheridia the first year. During the following years, archegonia and finally sporophytes were produced in normal numbers. The spores produced 2N gametophytes. After eleven years the race was completely fertile and was named *Bryum Corrensii*. Correlated with increasing fertility was a corresponding decrease in cell size so that by the time the race had achieved complete fertility its cell size had decreased to that typical of the original haploid (Wettstein 1937a, 1940; Wettstein & Straub 1942).

The reports of "sex chromosomes" in a number of dioicous species support the theory that sex determination in mosses is a phenomenon associated with the chromosomes. Many mosses possess one (or rarely two) chromosome from somewhat to much smaller than the others, which has been called an m-chromosome. A chromosome which is much larger than any of the others, termed an M-chromosome, occurs in some species. Either one or both size variations may be present in a particular species. These chromosomes may be heteropycnotic and the sex chromosome is often of the "m" or "M" type. Sex chromosomes have been positively identified in the following species: *Ceratodon purpureus* (Heitz 1932; Shimotomai & Kimura 1934, 1936; Jachimsky 1935), *Mnium punctatum* (Jachimsky 1935), *Pogonatum grandifolium* (Kurita 1937), *Pogonatum inflexum* (Shimotomai & Koyama 1932a,b), *Pogonatum spinulosum* (Kurita 1937) and *Polytrichum formosum* (*P. attenuatum*) (Shimotomai & Kimura 1934, 1936).

In his investigation of heterochromatin, Heitz (1928) studied 70 moss species representing 26 families and 47 genera. He found one or more heterochromosomes in most of the species investigated. His paper is relevant to this work, since a chromosome number or an estimated number of the chromosomes is given for each species studied. These numbers will be found in the list at the end of this section.

In a paper written in 1942, Heitz discusses the relation between polyploidy and monoicism in mosses. Twenty-six species of *Mnium* were considered, of which 17 were dioicous and 9 monoicous. He arranged the species in the following table (quoted in its entirety) which indicates possible relationships between dioicous haploid (or probably haploid) species and monoicous diploid (or probably diploid) species.

	<i>Getrenntgeschlechtlich</i>	<i>Gemischtgeschlechtlich</i>
Sekt. II.	<i>M. hornum</i> N = 6	
	<i>M. spinosum</i> N = 6	<i>M. spinulosum</i> (selten)
	<i>M. stellare</i> N = 7 (6 + 1)	
	<i>M. Blyttii</i>	
	<i>M. orthorhynchum</i> N = 6	
	<i>M. marginatum</i> fo. <i>dioica</i>	<i>M. marginatum</i> <i>M. adniviense</i>
Sekt. III.	<i>M. lycopodides</i>	
	<i>M. cuspidatum</i>	<i>M. cuspidatum</i> N = 12
	subspec. <i>trichomanes</i>	
	<i>M. affine</i> N = 6	<i>M. medium</i>
	<i>M. Seligeri</i> N = 6	
	(<i>M. insigne</i>	<i>M. insigne</i> var. <i>intermedium</i>)
	<i>M. rostratum</i> fo. <i>coriaceum</i>	<i>M. rostratum</i> N = 12
	<i>M. undulatum</i> N = 6	<i>M. Drummondii</i>
	<i>M. Maximoviczii</i> N = 7 (6 + 1)	
Sekt. IV.	<i>M. punctatum</i> N = 7	<i>M. pseudopunctatum</i> N = 13
	(6 + x), (6 + y)	(selten!) (12 + 1)
	<i>M. hymenophylloides</i> N = 7 (6 + 1)	
Sekt. V.	<i>M. cinclidioides</i>	

The above table is particularly interesting in regard to *Mnium punctatum* and *Mnium pseudopunctatum*. If, as Heitz says, *Mnium pseudopunctatum* arose by sporophytic regeneration of *Mnium punctatum* the expected chromosome number would be 14 ($12 + x + y$). He postulates hybridization between *Mnium punctatum* and some 6 chromosome race or related species, to account for the 13 chromosomes of *Mnium pseudopunctatum*.

Further papers of interest regarding the effects of polyploidy upon mosses, are those of Schmidt (1931) and Wettstein (1930, 1932). A spore from a tetraploid sporophyte of *Physcomitrium pyriforme* produced a plant having 18 chromosomes or half the normal haploid number. This hemiploid was self-fertile and regeneration of a sporophyte gave a 36-chromosome plant differing in various characters from typical *Physcomitrium pyriforme* ($N = 36$). The mating of the hemiploid with another hemiploid, presumed to have arisen in a similar fashion, followed by regeneration of the resulting sporophyte, produced plants indistinguishable from *Physcomitrium pyriforme*. The conclusion reached was that *Physcomitrium pyriforme* has two different sets of 18 chromosomes, either of which can produce a constant race.

Springer (1935) reported abnormal gametophytes of *Phascum cuspidatum* from $2N$ protonemata which gave rise to apogamous sporophytes from the stems and leaves. Spores produced by these sporophytes gave rise to normal and abnormal gametophytes. Springer concluded that meiosis had taken place in the apogamous sporophytes.

Barthelmess (1938) reported the production of over 100 mutations in *Physcomitrium pyriforme* by irradiation of spores with alpha and X rays. Many of the mutations were assumed to be heteroploid in nature because of the high degree of sterility present.

La Rue (1929) obtained protonemata and leafy plants by regenerating the young sporophytes of the following American species: *Amblystegium serpens*, *Aulacomnium heterostichum*, *Bryum caespitium*, *Catharina undulata*, *Cera-*

todon purpureus, *Ditrichum pallidum*, *Fissidens cristatus*, *Funaria hygrometrica*, *Mnium affine*, *Mnium cuspidatum*, *Mnium rostratum*, *Physcomitrium turbinatum*, *Polytrichum commune*, and *Polytrichum ohioense*. This work was done with the hope that data for American species similar to that of the Marchals and Wettstein for European species could be obtained. Unfortunately, the diploid gametophytes did not produce sex organs. The *Mnium* species reported to have been regenerated are of particular interest. La Rue found that *Mnium affine* was remarkably slow to regenerate and required 89 days before the beginning of protonematal growth. *Mnium cuspidatum* and *Mnium rostratum* were also reported as "very slow" to regenerate.

It is surprising that no cytotaxonomic work has been done on mosses, on the basis of the many experimental data which have accumulated. With regard to the following list of previously reported chromosome numbers in *Musci*, largely compiled from Tischler's lists (1927, 1931, 1936, 1938), but with additions by the author, it should be pointed out that numbers given for *Mnium* were determined, with one exception, from European or Asiatic representatives of the species.

It is interesting to note that all cases reported in the list of polyploidy within a species were experimentally produced. The naturally occurring polyploids all represent distinct species. This can be explained partially by the fact that many of the gametophytic characters used by taxonomists in delimiting moss species are those which are affected by polyploidy.

NAME OF MOSS	CHROMOSOME NUMBERS	SOURCE
SPHAGNACEAE		
<i>Sphagnum squarrosum</i>	20	Melín 1915
POLYTRICHACEAE		
<i>Polytrichum commune</i>	6	Vandendries 1912; Woodburn 1915
<i>Polytrichum commune</i>	7	Heitz 1928; Jachimsky 1935
<i>Polytrichum commune</i>	7 and 14	Kurita 1937
<i>Polytrichum juniperinum</i>	6	Drs. van Leeuwen-Reijnvaan 1907, 1908; Arens 1907; Allen 1912; Vandendries 1912
<i>Polytrichum juniperinum</i>	(6-)7	Heitz 1928
<i>Polytrichum juniperinum</i>	7	Kurita 1937
<i>Polytrichum piliferum</i>	6	Drs. van Leeuwen-Reijnvaan 1907, 1908; Vandendries 1912
<i>Polytrichum piliferum</i>	7	Heitz 1928
<i>Polytrichum formosum</i>	6	Drs. van Leeuwen-Reijnvaan 1907, 1908; Walker 1913
<i>Polytrichum gracile</i>	12-14	Heitz 1928
<i>Polytrichum alpinum</i>	7	Kurita 1937
<i>Polytrichum attenuatum</i>	7	Shimotomai and Kimura 1934, 1936
<i>Polytrichum attenuatum</i> var.	14	Kurita 1937
<i>Polytrichum</i> sp.	14	Kurita 1937
<i>Pogonatum urnigerum</i>	6-7	Heitz 1928
<i>Pogonatum urnigerum</i>	7	Kurita 1937
<i>Pogonatum grandifolium</i>	7	Kurita 1937
<i>Pogonatum nanum</i>	7	Jachimsky 1935
<i>Pogonatum spinulosum</i>	7	Kurita 1937

NAME OF MOSS	CHROMOSOME NUMBERS	SOURCE
POLYTRICHACEAE (cont.)		
<i>Pogonatum contortum</i>	7	Shimotomai and Koyama 1932a, 1932b
<i>Pogonatum inflexum</i>	7	Shimotomai and Koyama 1932a, 1932b
<i>Pogonatum rhopalophorum</i>	8	Ikeno 1904
<i>Catharinaea angustata</i>	8	Ikeno 1904
<i>Catharinaea angustata</i>	7	Kurita 1937
<i>Catharinaea undulata</i>	16-17	Wilson 1911
<i>Catharinaea undulata</i>	14-16	Heitz 1926
<i>Catharinaea undulata</i>	(20-)21 (-22)	Heitz 1928
<i>Catharinaea undulata</i>	21	Kurita 1937
<i>Catharinaea undulata</i>	14	Lowry, unpublished
<i>Catharinaea angustata</i>	7	Lowry, unpublished
BUXBAUMIACEAE		
<i>Buxbaumia aphylla</i>	7-8	Heitz 1928
FISSIDENTACEAE		
<i>Fissidens adiantoides</i>	(19)-21	Heitz 1928
DICRANACEAE		
<i>Dicranum japonicum</i>	11	Shimotomai and Koyama 1932a, 1932b
<i>Dicranum scoparium</i>	10-12	Heitz 1928
<i>Dicranum undulatum</i>	10-12	Heitz 1928
<i>Rhabdoweisia fugax</i>	ca. 12	Heitz 1928
DITRICHACEAE		
<i>Ceratodon purpureus</i>	11-12	Heitz 1928
<i>Ceratodon purpureus</i>	13	Shimotomai and Kimura 1934, 1936
<i>Ceratodon purpureus</i>	13	Jachimsky 1935
GRIMMIACEAE		
<i>Grimmia apocarpa</i>	>20	Heitz 1928
POTTIACEAE		
<i>Barbula fallax</i>	(9-)10 (-11)	Heitz 1928
SPLACHNACEAE		
<i>Splachnum sphaericum</i>	8	Schweizer 1923
<i>Splachnum sphaericum</i> var. <i>bivalens</i>	16	Schweizer 1923
<i>Splachnum ampullaceum</i>	8	Bornhagen 1930
<i>Splachnum ampullaceum</i> var. <i>bivalens</i>	16	Bornhagen 1930
<i>Splachnum ampullaceum</i> var. <i>quadrivalens</i>	32	Bornhagen 1930
FUNARIACEAE		
<i>Funaria hygrometrica</i>	14	Wettstein 1923, 1924a,b, 1930
<i>Funaria hygrometrica</i> var. <i>bivalens</i>	28	Wettstein 1924b
<i>Funaria hygrometrica</i> var. <i>quadrivalens</i>	ca. 56	Wettstein 1924b
<i>Funaria flavicans</i>	ca. 10	Beardsley 1931
<i>Funaria mediterranea</i>	26	Griesinger 1937
<i>Physcomitrella patens</i>	ca. 16	Wettstein 1924a
<i>Physcomitrium pyriforme</i> (hemiploid var.)	18	Wettstein 1930; Schmidt 1931
<i>Physcomitrium pyriforme</i> typ.	36	Wettstein 1930; Schmidt 1931
<i>Physcomitrium pyriforme</i> var. <i>tetravalens</i>	72	Wettstein 1930; Schmidt 1931
TIMMIACEAE		
<i>Timmia cucullata</i>	12	Scheuber 1932
<i>Timmia cucullata</i>	16	Lowry, unpublished
AULACOMNIACEAE		
<i>Aulacomnium palustre</i>	(9-)10	Heitz 1928
<i>Aulacomnium androgynum</i>	10-11	Heitz 1945
BARTRAMIACEAE		
<i>Philonotis fontana</i>	7-8	Heitz 1928
<i>Bartramia pomiformis</i>	7-8	Heitz 1928
<i>Bartramia pomiformis</i>	8	Kurita 1937
BRYACEAE		
<i>Bryum capillare</i>	10	Él. et Ém. Marchal 1911; Heitz 1928

NAME OF MOSS	CHROMOSOME NUMBERS	SOURCE
BRYACEAE (cont.)		
<i>Bryum capillare</i> var. <i>bivalens</i>	20	Él. et Ém. Marchal 1911
<i>Bryum caespiticium</i>	10	Él. et Ém. Marchal 1911; Wettstein 1924b
<i>Bryum caespiticium</i>	10 and 20	Griesinger (cit. Wettstein 1937a)
<i>Bryum Corrensii</i>	20 and 40	Griesinger (cit. Wettstein 1937a) and Griesinger 1937
<i>Bryum argenteum</i>	10	Ém. Marchal 1920
<i>Bryum argenteum</i>	10	Jachimsky 1935
<i>Bryum pseudotriquetrum</i>	9-10	Heitz 1928
<i>Webera nutans</i>	14	Heitz 1928
<i>Rhodobryum giganteum</i>	11	Shimotomai and Koyama 1932a, 1932b
MNIACEAE		
<i>Mnium hornum</i>	6	Wilson 1908, 1909, 1910, 1911, 1915; Él. et Ém. Marchal 1911; Heitz 1928; Jachimsky 1935
<i>Mnium hornum</i> var. <i>bivalens</i>	12	Él. et Ém. Marchal 1911
<i>Mnium affine</i>	8	Motte 1928
<i>Mnium affine</i> var. <i>ciliare</i>	6	Woodburn 1915
<i>Mnium</i> sp.	8	Drs. van Leeuwen-Reijnvaan 1908
<i>Mnium Maximoviczii</i>	7	Shimotomai and Koyama 1932a, 1932b
<i>Mnium undulatum</i>	6	Heitz 1942
<i>Mnium spinosum</i>	6	Heitz 1942
<i>Mnium Seligeri</i>	6	Heitz 1942
<i>Mnium orthorhynchum</i>	6	Heitz 1942
<i>Mnium cuspidatum</i>	12	Heitz 1942
<i>Mnium rostratum</i>	12	Heitz 1942
<i>Mnium stellare</i>	7	Heitz 1942
<i>Mnium hymenophylloides</i>	7	Heitz 1942
<i>Mnium punctatum</i>	7	Heitz 1928; Jachimsky 1935; Heitz 1942
<i>Mnium pseudopunctatum</i>	13	Heitz 1942
RHIZOGONIACEAE		
<i>Rhizogonium spiniforme</i>	6	Kurita 1937
<i>Rhizogonium Dozyanum</i>	7	Kurita 1937
LESKEACEAE		
<i>Thuidium japonicum</i>	10	Shimotomai and Koyama 1932a, 1932b
HYPNACEAE		
<i>Hypnum imponens</i>	6-7	Heitz 1928
<i>Ptilium crista-castrensis</i>	10	Kurita 1937
HYLOCOMIACEAE		
<i>Hylocomium squarrosum</i>	6-8	Heitz 1928
CLIMACEACEAE		
<i>Climacium japonicum</i>	11	Shimotomai and Koyama 1932a, 1932b
HOOKERACEAE		
<i>Hookeria lucens</i>	ca. 12	Heitz 1928
HYOPTERIGIACEAE		
<i>Hypopterigium japonicum</i>	18	Shimotomai and Koyama 1932a, 1932b
AMBLYSTEGIACEAE		
<i>Chrysohypnum stellatum</i>	6-8	Heitz 1928
<i>Calliergon cuspidatum</i>	(9-) 10	Heitz 1928
<i>Calliergon Richardsonii</i>	20	Heitz 1928
<i>Amblystegium serpens</i>	12	Él. et Ém. Marchal 1911; Wettstein 1924b
<i>Amblystegium serpens</i> var. <i>bivalens</i>	24	Él. et Ém. Marchal 1911; Ém. Marchal 1912; Wettstein 1924b

NAME OF MOSS	CHROMOSOME NUMBERS	SOURCE
AMBLYSTEGIACEAE (cont.)		
<i>Amblystegium serpens</i> var. <i>quadrivalens</i>	48	Él. et Ém. Marchal 1911
<i>Amblystegium irriguum</i>	12	Ém. Marchal 1912
<i>Amblystegium riparium</i>	24	Ém. Marchal 1912
BRACHYTHECIACEAE		
<i>Scleropodium purum</i>	9-10	Heitz 1928
<i>Eurhynchium Schleicheri</i>	8(-9)	Heitz 1928
<i>Eurhynchium rusciforme</i>	6-8	Heitz 1928
<i>Brachythecium velutinum</i>	10	Él. et Ém. Marchal 1911
FONTINALACEAE		
<i>Fontinalis antipyretica</i>	8	Heitz 1926
<i>Fontinalis antipyretica</i>	ca. 8	Heitz 1928

I wish to express my sincere appreciation to the following institutions and individuals for their valuable assistance and advice: to the University of Michigan for laboratory, library and other facilities, to the Horace H. Rackham School of Graduate Studies for financial aid in the form of a special fellowship; to Professor Ethel I. Sanborn of Corvallis, Oregon, Dr. Ruth D. Svihla of Seattle, Washington, Dr. Lewis E. Anderson of Durham, North Carolina, Dr. Frances E. Wynne of Chicago, Illinois, Dr. Ruth O. Schornherst of Tallahassee, Florida, and others, for the collection of specimens; to Dr. William C. Steere of the University of Michigan for verification of identifications and, as chairman of my committee, for much helpful advice and encouragement, and to the other members of my committee who have so kindly given their interest and valuable time to aid me in the completion of this work.

MATERIAL

The genus *Mnium* was selected for study for several important technical reasons. First, the number of representatives in North America is not so large as to make a complete survey of chromosome numbers and morphology impractical and is yet large enough so that the results should be of significance in considerations involving the entire genus. Secondly, over one-half of the 21 species known to occur in North America are found in Michigan, thus assuring an abundant supply of living material in natural habitats, within easy access. Thirdly, the species are easily maintained in the laboratory since they grow well if supplied with the proper light, temperature, and humidity.

METHODS

Including its embryonic leaves, the apical meristematic tissue of the gametophyte was used exclusively for the chromosome counts and observations of chromosome morphology, since cell divisions take place there over long periods of time. Because the haploid chromosome complement is present, counts are easier than in sporophytic material; furthermore the chromosomes are not so condensed as they are during meiosis and therefore reveal a more accurate picture of their morphology.

Plants collected in the spring during the active growth period were brought directly to the laboratory and placed in closed glass dishes, in order to assure them an atmosphere of high humidity. Light was supplied from a north window of the laboratory. Useful material was obtained until the production of sex organs, at which time mitosis in the apical meristematic region practically ceases. The production of sterile, stoloniform shoots in some species considerably prolongs the time in which cytological material can be obtained.

Plants collected in late summer and fall, with the exception of a few weedy species, for example, *Mnium cuspidatum*, *Mnium affine*, and *Mnium medium*, would not resume growth when placed in the customary cultural conditions. It was found necessary to "over-winter" these species in seed flats out-of-doors, after which active growth took place when the plants were brought into the laboratory early the following spring, about a month before growth was resumed by the same species under natural conditions.

Paraffin sections stained with iron-hematoxylin were first used (fig. 129), but it was soon found that the meristematic cells of the gametophyte and embryonic leaves contained large numbers of developing chloroplasts which stained deeply and made the observation of chromosomes extremely difficult. Gametophytes were fixed in a weak chrom-acetic solution (1 g. chromic acid and 2 ml. acetic acid to 100 ml. of water) for 24 hours, washed one hour in water and dehydrated by the glycerine method. Clearing was accomplished by means of a closely graded series of absolute alcohol-xylene mixtures. Infiltration with paraffin was also made very gradually by adding small amounts over a long period of time. The material was found to be extremely sensitive to changes in density of the various fluids, making precise technique necessary in order to avoid excessive shrinkage. Staining with crystal violet followed by an iodine mordant was tried, but it was found impossible to make the chromosomes retain sufficient stain for careful study, although iron-hematoxylin was found to produce good results. Because of their ease and rapidity of preparation, as well as their excellent quality, it was decided to use smear preparations exclusively.

For all counts and morphological studies of the chromosomes, the following smear technique was evolved and used, with slight modifications fitting it to the peculiarities of particular species. Gametophyte tips were cut off about 0.5 cm. from the apex and fixed in a mixture of 30 % glacial acetic acid plus 70 % absolute alcohol for at least one hour. It was found that material could be left in the fixing fluid for as long as 24 hours without affecting the subsequent staining properties. The apical meristem and embryonic leaves were isolated in a drop of stain (acetic orcein) on a slide and a cover glass was added. After the slide had been heated for approximately one minute, just below the boiling point of the stain, the cells were separated by tapping lightly on the cover glass with a bone needle handle. Any lateral movement of the cover glass at this point rolls the cells and breaks them, making the preparation useless. The cells were flattened, and excess stain removed, by placing the slide, cover glass down, on a pad of blotting paper and pressing on the back directly above the center of the

cover glass. The correct amount of pressure can be determined only by experience. Too little pressure does not spread the mitotic figures sufficiently to allow positive counts of the chromosomes and too great pressure breaks the cells and damages the chromosomes. The cover glass was sealed with vaseline and after an hour the chromosomes were sufficiently stained for study.

Slides made by the above technique remain in good condition for about one week, after that the cytoplasm gradually becomes colored by the stain, lowering the contrast of the preparation and eventually making it worthless.

Mounts may be made permanent by carefully removing the cover glass in 2 parts glacial acetic acid and 1 part absolute alcohol, dehydrating and clearing both cover glass and slide through the following solutions (Steere 1931): (1) 1 part glacial acetic acid + 2 parts absolute alcohol; (2) 1 part glacial acetic acid + 9 parts absolute alcohol; (3) absolute alcohol; (4) equal parts absolute alcohol and xylene. The slide and cover glass are reunited in thin xylene-balsam from the last solution. Although the moss material sticks to the slide and cover glass fairly well, caution is necessary during dehydration to prevent loss of material. Care is also necessary to prevent absorption of water vapor during the last two steps in dehydration and clearing before the addition of balsam.

Acetic orcein (0.5 % orcein + 0.1 % potassium acetate in 45 % acetic acid) was used in preference to aceto-carmin since it produced a more brilliant stain with moss chromosomes. The addition of the potassium acetate was found to increase noticeably the brilliance and stability of the stain.

The cells of some species of mosses were found to be excessively delicate, so that they break badly in the process of smearing. For these species, the following treatment improved the fixation and allowed good smears to be obtained: after being fixed for the usual one hour period in acetic-alcohol, the material was treated for 5–10 minutes in a solution of 30 ml. of glacial acetic acid, 65 ml. of absolute alcohol, and 5 ml. of formalin. Smears were made after washing for five minutes in acetic alcohol. Too long a treatment with the formalin solution should be avoided because it causes the cytoplasm to stain deeply.

When the cells would not separate readily from one another, it was found that a 5–10-minute immersion, after fixing, in a solution consisting of equal parts of concentrated hydrochloric acid and 95 % alcohol, followed by a 15-minute immersion in acetic alcohol, made a noticeable improvement (Warmke 1935). This method does not produce as good results with moss tissue as it does with root-tip meristems of the flowering plants, perhaps because of differences in the chemical nature of the middle lamella in the two plant groups.

In this study, temporary smears were preferred to permanent slides, since division figures at best are not numerous and the danger of losing them during dehydration is great. The smears were studied and drawings made as soon as possible after their completion.

Smears of the meiotic division in the spore-mother cells were prepared by the following technique. It was found through experiment that meiosis occurs

at about the time the capsule has assumed its mature form and size, but is still bright green. The capsule wall was cut open and the columella with the adhering spore-mother cells was dissected out and fixed for 15 minutes in an acetic-alcohol solution. After fixation the mass of tissue was placed in a drop of acetic orcein on a slide, covered, and the spore-mother cells separated from the tissue of the columella and from each other by tapping on the cover glass with a needle handle. The cover glass was then sealed with vaseline.

A phase-plate filter, having its maximum transmission in the green region of the spectrum, was used between the light source and microscope condenser for all observations because it improved the contrast and visibility of the chromosomes.

All drawings were made with a camera lucida at a magnification of 2000 diameters.

The leaf-cell size of the species-pairs was obtained by using Amann's (1921) technique, which consists of determining the average number of cells per square mm. (cell index). The procedure was as follows: a metal disc, with a 1.5 mm. square aperture in its center, was placed in the ocular of the microscope. The exact area of the field included in the aperture was determined for the various objectives, by means of a stage micrometer slide. The number of cells included within the aperture was counted and by multiplying the result by an appropriate factor the number of cells per square mm. was obtained. All measurements were made in an area halfway between the leaf base and apex and halfway between the leaf border and costa.

RESULTS

A short description, including only important diagnostic characters, is presented for each species studied. The descriptions are condensed versions of those given by Andrews in the *Moss flora of North America* (1940) and have been compared with actual specimens. After the description the following data are listed: geographical distribution, specimen number and collection location for the material studied, chromosome number, chromosome measurements, and notes on the location of spindle attachment regions when such data are available. The cell index is also given for some species.

A tabular summary listing chromosome numbers and average chromosome lengths is included at the end of this section.

MNIMUM Hedw. Plants dioicous or synoicous; stems normally erect; leaves of most species with a border of elongated cells, one or more cells in thickness, frequently with single or double teeth; costa strong, but not always reaching the leaf-apex; cells tending to be hexagonal, their walls sometimes thickened or pitted.

Sporophytes single or several from the same perichaetium. Capsules horizontal to pendulous, oblong to oval; neck short; stomata usually confined to neck, cryptopore; operculum convex to rostrate; teeth of outer peristome 16, of approximately same length as inner peristome, strong, not united at base, tending to be bordered, papillose; dorsal longitudinal line zig-zag, dorsal plates low; ventral lamellae numerous; inner peristome yellow to reddish brown, with

high basal membrane which is in some species irregularly perforated; segments tapering to a mostly slender, cuspidate apex, broadly fenestrate to gaping; cilia mostly in 3's, nodulose. Type species, *Mnium hornum* (Andrews 1940).

MNIUM MENZIESII (Hook.) C. Müll. Plants dioicous, 4–8 cm. high, dendroid, with numerous small branches from upper part, the branches slender, spreading, often decurved, rarely reaching 2 cm. in length; stem leaves in lower part of stem distant, erect, closely appressed to stem, small and scale-like, whitish-hyaline at least in upper part of leaf, slenderly lanceolate, long-acuminate, decurrent, dentate throughout with slender, single-celled teeth which stand out at right angles or nearly so to edge of leaf; costa broader at base, slender above, not reaching apex, not toothed; leaf cells in basal part of leaf chlorophyllose, more or less rectangular, rather small, up to $35 \times 15 \mu$, thick-walled, in upper, hyaline part of leaf the cells much longer, up to 100μ , thin-walled and empty of chlorophyll, the teeth in this part being only the projecting distal ends of elongated border cells, without, however, a distinctly differentiated border being formed. On upper part of stem the leaves less distant, broader, with normal, irregularly rounded, hexagonal, chlorophyllose cells, except in acuminate point; teeth shorter and less prominent; costa stronger, slightly toothed dorsally. The branches issue from the stem at an angle between 45° and 90° , slightly above the axils of the upper stem-leaves, normally one to each leaf-axil; the branches are simple or themselves slightly branched, their leaves are closer, erect-spreading, more ovate-lanceolate, with short acute apex, not hyaline, sharply toothed, especially in upper part; costa also sharply toothed dorsally, decurrent; cells chlorophyllose throughout.

Seta erect, strong, somewhat flexuose, reddish, to 5 cm. high; capsules single or 2, rarely 3, from the same perichaetium, more or less pendulous, up to 8 mm. in length, oval-cylindric, yellowish-green to brown; operculum hemispheric, mamnillose at apex; stomata in neck of capsule, cryptopore; outer and inner peristome of approximately equal length, both dark yellow; spores round, greenish-yellow, about 30μ , papillose, ripening in spring.

Alaska to northern California, inland to Idaho.

The following specimen was studied:

No. 6. Collected in Seattle, Washington, by Dr. Ruth D. Svihla. $N = 5$.

The gametophytic chromosome number is 5 (figs. 1–10). The chromosomes are 0.75μ wide and their average lengths are as follows: 7.4μ , 6.6μ , 5.6μ , 5.2μ , 4.6μ .

MNIUM STELLARE Hedw. Plants dioicous, 2–3 cm. high; fertile stems simple, erect; sterile stems frequently curved; leaves elliptic-ovate, obtuse to short-pointed, decurrent, not bordered, but outer 1–2 rows of cells may be somewhat elongated or slightly darker-pigmented, upper leaves denticulate on their apical border with broad unicellular teeth which project normally not in the plane of the leaf-blade, but at angles to it on either side; costa ceasing abruptly at some distance from the apex; cells of leaf 20–30 μ in diameter, walls with thickened corners.

Explanation of figures 1–28

FIGS. 1–10. *Mnium Menziesii*. FIGS. 1–9. Chromosomes in metaphase. FIG. 10. Chromosomes in late metaphase showing longitudinal division. FIGS. 11–21. *Mnium stellare*. FIGS. 11–19. Chromosomes in metaphase. FIG. 20. Chromosomes in early anaphase showing spindle-attachment regions. FIG. 21. Chromosomes in late metaphase showing spindle-attachment regions. FIGS. 22–24. *Mnium hornum*. Chromosomes in metaphase. FIGS. 25–28. *Mnium orthorhynchum*. Chromosomes in metaphase. All figures $\times 1332$.



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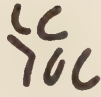
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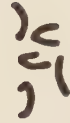
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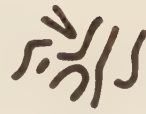
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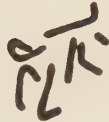
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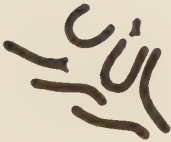
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Sporophytes* single; seta about 2 cm. high; capsule pendulous, oblong with short neck, somewhat bent and asymmetric, brownish green, up to 3 mm. long; operculum convex, not pointed; stomata in neck; outer peristome-teeth greenish-yellow; inner peristome dark yellow.

Spores* 20 μ , greenish yellow, ripening in May or June.

New Brunswick and Ontario south to Virginia, west to Minnesota; also in Europe and Asia.

The following specimens were examined:

No. 1. University of Michigan Biological Station, Cheboygan, Michigan.
N = 7.

No. 22. Nichol's Arboretum, Ann Arbor, Michigan. N = 7.

No. 23. Cady's Corners, Washtenaw County, Michigan. N = 7.

The specimens agree closely with the description and are typical of the species.

The haploid chromosome number of *Mnium stellare* as determined from the specimens listed above, is 7.

The average chromosome lengths are as follows: 12.1 μ , 10.6 μ , 10 μ , 9.9 μ , 7 μ , 6.3 μ , 1.8 μ . The spindle-fiber-attachment regions are located as follows: In the long group three chromosomes have approximately median attachment regions, the fourth has a submedian attachment; of the two medium-length chromosomes one is attached terminally and the other subterminally; the short chromosome has a terminal attachment region.

The over-all size of the chromosomes is large compared with those of the other *Mnium* species.

MNIUM HORNUM L. Plants dioicous, to 7 or 8 cm. high; stem usually simple, slender, more or less erect, but often somewhat flexuose; leaves, narrowly elliptic-ovate, somewhat decurrent, sharply acute to short-acuminate, with a swollen border of darker, narrow cells, more than one cell in thickness, with numerous, double, short but sharp teeth; costa not reaching apex, somewhat toothed dorsally; cells of leaf averaging 20–25 μ , tending to be isodiametric except in basal part where they become somewhat elongated with more thickened corners.

Sporophytes single; seta 2–3 cm. high; capsules horizontal to pendulous, oblong, symmetric, about 4 mm. long, greenish-brown, abruptly narrowed into a short, darker-colored neck; stomata in neck; outer peristome-teeth greenish-yellow; inner peristome orange-yellow.

Spores greenish-yellow, 25–30 μ , roughened, ripening in summer.

Labrador to Georgia, west to Ohio and Tennessee: collected once in Missouri.

Plants of the following collection were studied.

No. 24. Thunderhole Creek, tributary of John's River, near Upton, Caldwell County, North Carolina. Collected by H. L. Blomquist. N = 6.

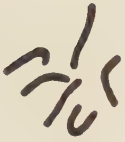
The plants of the collection do not differ from the description and well represent this distinct and stable species.

The chromosomes are about 0.5 μ in width and their average lengths in microns are as follows: 5.7, 5.5, 5.2, 5, 4.5, 4.

* Not seen by the author

Explanation of figures 29–56

FIGS. 29–36. *Mnium orthorhynchum*. FIGS. 29–35. Chromosomes in metaphase. FIG. 36. Chromosomes in late metaphase showing spindle-attachment regions. FIGS. 37–48. *Mnium marginatum*. Chromosomes in metaphase. FIGS. 49–56. *Mnium spinulosum*. Chromosomes in metaphase. All figures $\times 1332$.



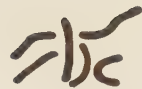
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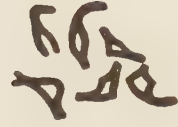
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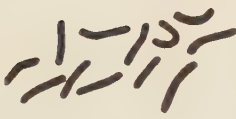
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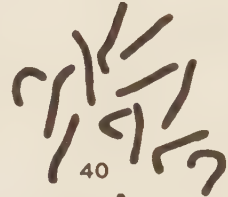
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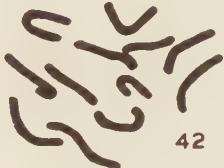
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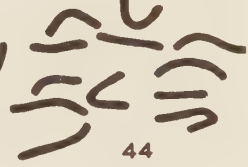
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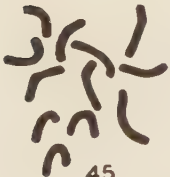
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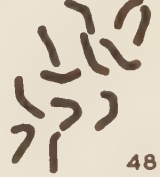
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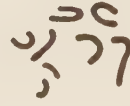
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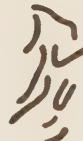
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MNIUM ORTHORHYNCHUM Brid. Plants dioicous, 1–2 cm. high; fertile stems simple, erect; sterile stems flexuose, not much longer than others; leaves, oblong-ovate, acute to short-apiculate, decurrent, bordered throughout with thickened border of elongated cells in more than one layer, toothed throughout with double teeth; costa percurrent, joining border to form apiculus, toothed dorsally in upper part, especially in the apical and perichaetial leaves; cells of leaf small, rarely exceeding 20 μ , walls with corners slightly if at all thickened.

Sporophytes single; seta about 2 cm. long; capsules approximately horizontal, oblong-cylindric, straight, urn 3 to 4 mm. long, reddish-brown when ripe, contracted abruptly into a short narrow neck; operculum short-rostrate, about 1.5 mm. long; stomata in neck; outer peristome-teeth light yellow below, darker toward apex; inner peristome golden yellow.

Spores greenish-yellow, 30–40 μ , slightly roughened, ripening in summer.

Widely distributed through the three northern continents in North America from Alaska and Yukon south to New Mexico, in the eastern states to North Carolina.

The following specimens were studied:

No. 4. Archegonial plants, Nichol's Arboretum, Ann Arbor, Michigan.
N = 6.

Gametophytic characters agree well with the description. The teeth on the back of the costa, although definitely present, were not so strongly developed as in other collections seen by the author.

The haploid chromosome number of *Mnium orthorhynchum*, as represented by the above specimen, is 6 (figs. 25–36).

The average lengths of the six chromosomes are as follows: 7.2 μ , 6.7 μ , 6.3 μ , 5.8 μ , 5.5 μ , 5 μ . The average width of the chromosomes is 0.75 μ .

The spindle-attachment regions all seem to be median or submedian except one which is either subterminal or terminal (fig. 30).

The leaf cells average 2578 per square mm.

MNIUM MARGINATUM (Dicks.) Beauv. Plants synoicous, to 3 cm. high; fertile stems simple erect; sterile stems flexuose, often twice as long as others; leaves oblong-ovate, short-acuminate, decurrent, bordered throughout with thickened border of narrow cells in more than one layer, toothed throughout with short, double teeth; costa percurrent and joining border to form apiculus; cells of leaf up to 35 μ , walls with thickened corners.

Sporophytes single; seta to 2 cm. high; capsule approximately horizontal, brownish-yellow, oblong-cylindric, sometimes slightly curved, abruptly narrowed into slender neck, urn to 5 mm. long; operculum rostrate, to 2 mm. long; stomata in neck; outer peristome-teeth rusty brown; inner peristome brown.

Spores yellow, about 25 μ or slightly more, finely roughened, maturing in May.

Widely distributed in the three northern continents; in our eastern states

Explanation of figures 57–84

FIGS. 57–60. *Mnium spinulosum*. FIGS. 57–59. Chromosomes in metaphase. FIG. 60. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. FIGS. 61–66. *Mnium Drummondii*. FIGS. 61–65. Chromosomes in metaphase. FIG. 66. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. FIGS. 67–78. *Mnium cuspidatum*. FIGS. 67–73. Chromosomes in metaphase. FIGS. 74, 75. Chromosomes in anaphase. FIG. 76. Chromosomes in late metaphase showing spindle-attachment regions. FIGS. 77, 78. Bivalent chromosomes of the first meiotic metaphase. FIGS. 79–84. *Mnium cuspidatum* (N = 6). Chromosomes in metaphase. All figures $\times 1332$.



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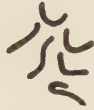
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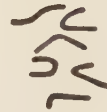
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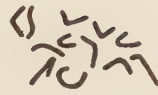
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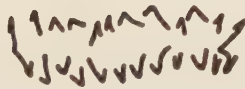
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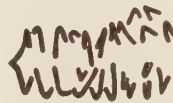
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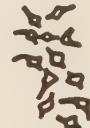
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south to Tennessee, the central states to Missouri, in the west from the Yukon south to Arizona and New Mexico.

The following specimens were studied:

No. 3. School Girl's Glen, Nichol's Arboretum, Ann Arbor, Michigan. Collected by L. Holdridge. $N = 12$.

The twelve chromosomes are divided into six pairs, the members of each pair being of the same length. The average lengths of the six pairs are as follows: 7.3 μ , 6.4 μ , 6.0 μ , 5.6 μ , 5.2 μ , 4.7 μ . The average width of the chromosomes is 0.75 μ (figs. 37-48).

The leaf cells average 2349 per square mm.

MNIUM SPINULOSUM Br. and Sch. Plants synoicous, about 1 cm. high; stems erect, simple; leaves broadly obovate from a narrow base, short cuspidate, decurrent, border throughout with a very strong, thick border which is round in section, its inner cells stereid, toothed in upper part of leaf with long, sharp, double teeth, costa slightly excurrent; leaf cells 18-25 μ , walls without thickened corners.

Sporophytes single in eastern United States, 2 or 3 in western United States and Europe; seta 2.3 cm. high; capsule pendulous, urn oblong-cylindric, straight, about 3 cm. long, very light straw-color, dark brown to purplish at mouth, abruptly narrowed into slender neck which passes gradually into thickened and hooked summit of seta; operculum conic-rostrate; stomata in neck; outer peristome-teeth dark purplish-brown; inner peristome-teeth brown.

Spores brownish-yellow, 15-20 μ , minutely roughened, ripening in May to June.

In Europe, from Pyrenees through the Alps to the eastward, uncommon. Not rare in North America, Nova Scotia to Maryland in the east, westward to Pacific coast from Alaska to Oregon.

Specimens studied:

No. 8. University of Michigan Biological Station, Cheboygan, Michigan. $N = 8$.

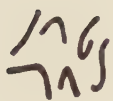
The average lengths of the eight chromosomes are as follows: 6.8 μ , 6.6 μ , 5.8 μ , 5.4 μ , 4.8 μ , 4.2 μ , 2.6 μ , 2.1 μ . The average width of the chromosomes is 0.75 μ (figs. 49-60).

There appears to be at least one long chromosome with a terminal attachment region. The attachment regions of the two small chromosomes appear to be terminal. The remaining members of the complement have median or submedian attachments (fig. 60).

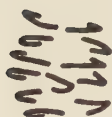
MNIUM DRUMMONDII Br. & Sch. Plants normally synoicous, but large antheridial heads with broad perigonal leaves and more or less clavate paraphyses may also occur, even in the same tuft with the synoicous plant, to 2 cm. high; fertile stems simple erect, sterile stems somewhat stoloniform, leaves broadly obovate-spatulate, short-acuminate, decurrent, bordered by 2-4 rows

Explanation of figures 85-112

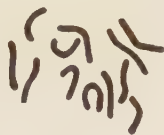
FIGS. 85-86. *Mnium cuspidatum* ($N = 6$). FIG. 85. Chromosomes in metaphase. FIG. 86. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. FIGS. 87-98. *Mnium medium*. FIGS. 87-95, 97, 98. Chromosomes in metaphase. FIG. 96. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. FIGS. 99-110. *Mnium insigne*. FIGS. 99-107. Chromosomes in metaphase. FIG. 108. Chromosomes in late metaphase showing spindle-attachment regions. FIGS. 109, 110. Chromosomes in anaphase. FIGS. 111, 112. *Mnium cinclidioides*. Chromosomes in metaphase. All figures $\times 1332$.



85



86



87



88



89



90



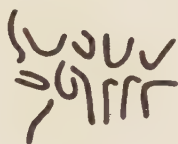
91



92



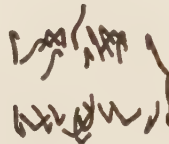
93



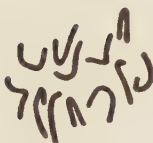
94



95



96



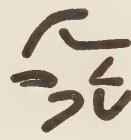
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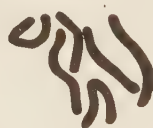
101



102



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104



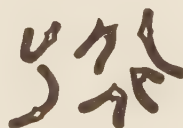
105



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107



108



109



110



111



112

of elongated cells in single thickness, toothed in upper half of leaf only with single, sharp teeth mostly of one cell each; costa percurrent; cells of leaf distinctly hexagonal, to 40 μ , walls not pitted, corners not thickened.

Sporophytes 1-4 or even 5 from the same perichaetium; capsule pendulous, oblong, urn 3 mm. or less, light yellow, neck short and inconspicuous; operculum convex with a sharp point; stomata in neck; outer peristome-teeth light greenish-yellow; inner peristome brownish-yellow.

Spores yellow, papillose, ca. 22 μ , ripening in May or June.

From Maine to Washington in a narrow belt across the continent, somewhat northward into Canada. In the east southward to Maryland and Pennsylvania; in northeastern Europe and reported from Siberia.

Specimens studied:

No. 15. University of Michigan Biological Station, Cheboygan, Michigan. N = 6.

The average length of the chromosomes is as follows: 5.9 μ , 5.4 μ , 5.2 μ , 5.1 μ , 4.9 μ , 4.5 μ . The average chromosome width is 0.5 μ .

The spindle attachment regions are all median or submedian (fig. 66).

MNIUM CUSPIDATUM Hedw. Plants synoicous, approximately 2 cm. high; fertile stems simple, erect; sterile stems generally much longer than fertile stems, stoloniform, leaves complanate; leaves obovate from a narrow base, acute to short-acuminate, decurrent, bordered by 2-4 rows of narrow cells in single thickness, toothed in upper half only with single, sharp teeth, composed of single cells; costa percurrent; cells up to 25 μ in longest diameter, walls pitted, with thickened corners.

Sporophytes single; to 3 cm. high; seta curved below capsule neck; capsule pendulous, oblong to oval, urn to 3.5 mm. long, yellow to brownish-yellow when mature, neck very short; operculum high-convex without noticeable point; stomata in neck; outer peristome-teeth greenish-yellow; inner peristome brown, basal membrane very conspicuously lacunose.

Spores yellow, 20-25 μ , slightly papillose, ripening in April and May.

Common throughout the United States and northward into Canada, also in Europe and Asia.

Specimens studied:

No. 19. Nichol's Arboretum, Ann Arbor, Michigan. N = 12.

No. 14. Waterloo, Michigan. Collector E. A. Phillips. N = 12.

No. 13. *Mnium cuspidatum*, Florida. Collector Dr. Ruth O. Schornherst. N = 6.

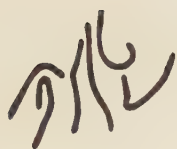
The average length of the six chromosome pairs of *Mnium cuspidatum* is as follows: 6.4 μ , 5.6 μ , 5.2 μ , 4.8 μ , 4.4 μ , 4.1 μ . The chromosomes are 0.5 μ wide. The spindle attachment regions are all median or submedian (figs. 74, 76).

Mnium cuspidatum regularly shows 12 bivalents at metaphase I (figs. 77-78).

No. 13 differs from typical *Mnium cuspidatum* chiefly in its smaller size.

Explanation of figures 113-140

FIGS. 113-120. *Mnium cinclidioides*. FIGS. 113-118. Chromosomes in metaphase. FIGS. 119, 120. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. FIGS. 121-129. *Mnium affine*. FIGS. 121-125, 127. Chromosomes in metaphase. FIG. 126. Chromosomes in late metaphase showing spindle-attachment regions. FIG. 128. Chromosomes in anaphase. FIGS. 130-132. *Mnium affine* var. *ciliare*. FIGS. 130, 131. Chromosomes in metaphase. FIG. 132. Chromosomes in late metaphase showing spindle-attachment regions. FIGS. 133-140. *Mnium punctatum*. Chromosomes in metaphase. All figures $\times 1332$.



113



114



115



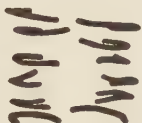
116



117



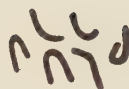
118



119



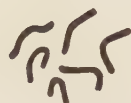
120



121



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123



124



125



126



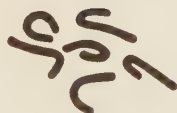
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137



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139



140

The leaves are less strongly decurrent and the leaf cell size is smaller, 2881 cells per square mm. in contrast to 1885. The chromosome number is 6 (figs. 79–86). The average chromosome lengths are as follows: 6.6 μ , 6.3 μ , 6.1 μ , 5.3 μ , 4.9 μ , 4.6 μ . The spindle-attachment regions are all median or submedian (fig. 86).

MNIUM MEDIUM Br. and Sch. Plants synoicous, approximately 3 cm. high; fertile stems simple, erect; sterile stems not much longer than others, deflexed; leaves broad-oval to slightly obovate, short-cuspidate, decurrent, bordered by 2–3 rows of narrow cells in single thickness, toothed throughout with single, sharp teeth of one cell each; costa percurrent, combining with border to form cuspidate apex; cells of leaf reaching 80 μ near costa, walls prominently pitted with distinct corner-thickenings.

Sporophytes 1–3 from the same perichaetium; seta to 5 cm. long; capsule pendulous, oblong; urn 3–4 mm. long, yellow to light brown, with short and inconspicuous neck; operculum convex, apiculate; stomata in neck; outer peristome-teeth yellow; inner peristome orange, basal membrane not perforated.

Spores dark yellow, 20–25 μ , papillose, ripening in April and May.

New England to Washington, south to Maryland and California, northward through Canada to Alaska, Yukon and Greenland; also in Europe and Asia.

The following specimens were studied:

No. 7. Cascade Glen, Ann Arbor, Michigan. Collector, W. C. Steere. N = 12.

No. 12. Stinchfield Woods, Washtenaw County, Michigan. N = 12.

No. 25. University of Michigan Biological Station, Cheboygan, Michigan. N = 12.

The gametophytic chromosome number is 12 (figs. 87–98). The 12-chromosome complement consists of 6 pairs, the members of each pair being of equal length. The average lengths of the 6 chromosome pairs are as follows: 6.4 μ , 5.7 μ , 5.3 μ , 5.0 μ , 4.6 μ , 4.1 μ . The chromosomes are 0.5 μ + wide. The spindle-attachment regions are median or submedian (fig. 96).

There are 575 leaf cells per square mm.

MNIUM AFFINE Bland. Plants dioicous, approximately 3 cm. high; fertile stems simple, erect; sterile stems much longer than others, stoloniform often rooting at tip, leaves complanate; leaves oval to obovate, short-cuspidate, often weakly decurrent, bordered by 2–4 rows of narrow cells in single thickness, usually toothed throughout with sharp teeth of 1–3 cells each, the teeth in some forms much reduced to almost lacking; costa percurrent, ending in cuspidate apex; cells of leaf up to 50 μ in longest diameter, walls pitted, corners not strongly thickened.

Sporophytes mostly single, rarely 2–3 from the same perichaetium; seta about 3 cm. long; capsule pendulous, oblong, about 5 mm. long, brownish-yellow, neck short and inconspicuous; operculum short-convex or broadly conic, apiculate; stomata in neck; outer peristome-teeth greenish-yellow; inner peristome orange, basal membrane not perforated.

Spores yellow, 25 μ , papillose, ripening in spring.

Common throughout the United States and northward to Greenland and Alaska, also in Europe and Asia.

The following specimens were studied:

No. 16. University of Michigan Biological Station, Cheboygan, Michigan. N = 6.

No. 9. University of Michigan Biological Station, Cheboygan, Michigan. N = 6.

No. 10. Little Portage Lake, Washtenaw County, Michigan. $N = 6$.

No. 18. Nichol's Arboretum, Ann Arbor, Michigan. $N = 6$.

The gametophytic chromosome number is 6 (figs. 121-132). The average length of the chromosomes for typical *Mnium affine*, as represented by Nos. 16, 10, and 18, are as follows: 6.5 μ , 6 μ , 5.6 μ , 5.2 μ , 4.8 μ , 4.3 μ . The chromosomes are 0.5+ μ wide. Spindle-attachment regions are median or submedian (figs. 126, 128).

No. 9 represents the variety *ciliare*, characterized by the long, multicellular teeth of the leaf margin and by its more robust growth habit. The chromosomes are larger than those of the species (figs. 130-132). The average chromosome lengths are as follows: 8.6 μ , 7.6 μ , 7.4 μ , 7.1 μ , 6.7 μ , 6.3 μ . The spindle-attachment regions are median to submedian (fig. 132).

There are 615 leaf cells per square mm.

MNIUM INSIGNE Mitt. Plants dioicous, very robust, approximately 6 cm. in height; fertile stems simple, erect; sterile stems deflexed; leaves narrowly elliptic, acuminate, prominently long-decurrent, bordered by mostly 3 rows of narrow cells in single thickness, toothed throughout, teeth of lower part of leaf short and blunt, those of apical part sharp, mostly of a single cell each; costa percurrent or nearly so; cells of leaf up to 50 μ in diameter, walls pitted, corners strongly thickened.

Sporophytes 1-9 from the same perichaetium, most frequently 3-6; seta approximately 3 cm. long; capsule pendulous, oblong, about 5 mm. long, yellowish-brown when ripe, neck short; operculum broadly conic, apiculate to almost short-rostrate; stomata in neck; outer peristome-teeth greenish-yellow; inner peristome orange, basal membrane not perforated.

Spores dark yellow, papillose, about 25 μ , ripening in April or May.

Alaska to northern California, inland to northwestern Montana.

The following specimen was studied:

No. 5. Seattle, Washington. Collector, Dr. Ruth D. Svihla. $N = 6$.

The gametophytic chromosome number is 6 (figs. 99-110). The chromosomes are large, 1 μ wide, and their average lengths as follows: 10 μ , 9.4 μ , 8.8 μ , 8.5 μ , 7.9 μ , 7.3 μ . The spindle-attachment regions are median to submedian (figs. 108-110).

MNIUM CINCLIDIODES Huben. Plants dioicous, up to 5 cm. or more in height; fertile stems simple, erect or slightly flexuose; sterile stems erect, flexuose; leaves complanate, obovate, rounded or with a short, blunt point, without a distinct border, though the cells of border region are gradually narrowed in several rows and may show a few short, blunt teeth; costa not reaching apex; cells of leaf so elongated in oblique direction from costa outward as to appear rhomboidal, up to 125 $\times$ 30 μ near costa, walls pitted, corners not thickened.

Sporophytes usually single; seta to 6 cm. or more in height; capsule pendulous, oval, with short neck, passing into thickened and much crooked top of seta, urn about 3 mm. long, brown when ripe; operculum convex, apiculate; stomata in neck; outer peristome-teeth brown; inner peristome yellowish-brown.

Spores 35 μ , brownish-yellow, minutely roughened, ripening in May-June.

Greenland to Alaska, southward in peat-bogs to Connecticut, New Jersey, Pennsylvania, Michigan, Minnesota, Montana, British Columbia; also in Europe and Northern Asia.

The following specimen was studied:

No. 11. University of Michigan Biological Station, Cheboygan, Michigan. $N = 6$.

The gametophytic chromosome complement of 6 is characterized by one chromosome noticeably longer than the others (figs. 111–120). The average chromosome lengths are as follows: 10.3 μ , 7.6 μ , 7.2 μ , 6.5 μ , 5.8 μ , 5.2 μ . The chromosomes are about 0.5 μ in width. The spindle-attachment regions are median to submedian with one subterminal (figs. 119–120).

MNIUM PUNCTATUM Hedw. Plants generally dioicous, varying to synoicous, to 5 cm. or occasionally more in height; leaves large, not or but slightly decurrent, oval to more commonly obovate-spatulate, broadly rounded to slightly emarginate at apex, with a distinct border, not toothed, the border sometimes reddish, 1 or more layers of narrow cells, 1 or more cells wide; costa fairly strong, ceasing below apex or percurrent, sometimes uniting with border to form a short, blunt point at apex, cells of leaf irregularly hexagonal to nearly rhomboidal, frequently elongated and arranged in rows in oblique direction from costa to border, to $150 \times 50 \mu$, sometimes half as large or less, walls thin without pits or thicker and pitted, corners not or slightly thickened.

Capsules generally single, horizontal to pendulous, ovoid to oblong-cylindric, light yellowish to brownish, up to 5 mm. long when deoperculate, neck short; operculum conic-rostrate; stomata in neck of capsule, cryptopore; outer peristome-teeth brown to yellow; inner peristome golden yellow, basal membrane high, not perforated; spores 35–40 μ , brownish-yellow, roughened, ripening in winter or spring.

Greenland to Alaska, southward to Georgia, Ohio, Michigan, Wisconsin, Minnesota, Colorado, California; also in Europe and Asia.

The following specimens were studied:

No. 2. University of Michigan Biological Station, Cheboygan, Michigan. $N = 7$.

No. 17. Lake City, Michigan. $N = 14$.

No. 20. Corvallis, Oregon. Collected by Professor Ethel I. Sanborne. $N = 6$.

No. 2 is the typical dioicous *Mnium punctatum*. The gametophytic chromosome number is 7 (figs. 133–144). The average chromosome width is 0.3 μ and the average chromosome lengths are as follows: 4.7 μ , 4.3 μ , 3.9 μ , 3.6 μ , 3.2 μ , 2.7 μ , 0.9 μ .

There are 465 leaf cells per square mm.

No. 17 is a synoicous form referable to *Mnium pseudopunctatum*. The gametophytic chromosomes consist of 7 pairs. The average chromosome width is 0.3 μ and the average length of the 7 pairs is as follows: 4.8 μ , 4.5 μ , 4 μ , 3.7 μ , 3.2 μ , 2.7 μ , 0.75 μ (figs. 145–149). The spindle-attachment regions seem to be mainly median, submedian, or subterminal. Two of the long chromosomes appear to have terminal attachment regions (fig. 149).

There are 390 leaf cells per square mm.

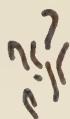
No. 20 is referable to Kindberg's *Mnium glabrescens*. The gametophytic

Explanation of figures 141–167

FIGS. 141–144. *Mnium punctatum*. Chromosomes in metaphase. FIGS. 145–149. *Mnium pseudopunctatum*. FIGS. 145–148. Chromosomes in metaphase. FIG. 149. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. FIGS. 150–158. *Mnium glabrescens*. FIGS. 150–157. Chromosomes in metaphase. FIG. 158. Anaphasic chromosomes. FIGS. 159–167. *Cinclidium stygium*. FIGS. 159–165. Chromosomes in metaphase. FIGS. 166, 167. Chromosomes in anaphase showing the approximate locations of the spindle-attachment regions. All figures $\times 1332$.



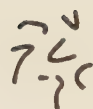
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142



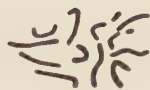
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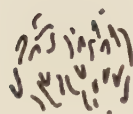
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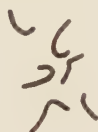
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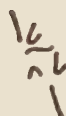
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153



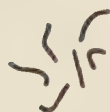
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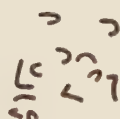
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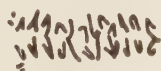
163



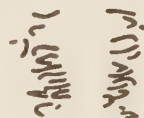
164



165



166



167

chromosome number is 6 (figs. 150–158). The chromosomes are $0.3\ \mu$ wide and their average lengths are as follows: $4.7\ \mu$, $4.2\ \mu$, $3.7\ \mu$, $3.6\ \mu$, $3.4\ \mu$, $2.4\ \mu$. There are no clear indications of terminal spindle-attachment regions.

There are 480 leaf cells per square mm.

CINCLIDIUM Sw. Not differing from *Mnium* in its gametophytic characters. All species have entire bordered leaves. The capsule differs in its peristome; the exostome having shorter blunt teeth, the endostome not divided as normally into segments and cilia, but consisting of a single dome-like structure with small round openings at apex and somewhat irregular openings at the side, corresponding in number and position with the outer peristome-teeth. Spores rather large. Type species *Cinclidium stygium* Sw. (Andrews 1940).

CINCLIDIUM STYGIUM Sw. Plants synoicous, 3 cm. high or sometimes higher; stems stout, erect, simple or occasionally branching subapically; leaves of good size, from a very narrow base broadly oval to obovate, sharply apiculate, with a reddish border of 3 to 4 rows of very narrow thick-walled cells; costa strong, reddish, generally extending into apex; cells of leaf, except those immediately adjacent to costa or border, elongated in oblique or transverse direction from costa to border, irregularly elongated-hexagonal, to $50 \times 30\ \mu$, rather thick-walled without thickened corners, walls pitted.

Seta slender, erect, flexuose, 3 or 4 cm. long or sometimes longer, reddish-yellow, thickened and strongly crooked where it passes into neck of capsule; single, pendulous, up to 4 mm. long, oval-pyriform with prominent, broad neck about one-third length of entire capsule, light yellowish-brown when mature; operculum hemispheric; stomata in neck of capsule, cryptopore; outer peristome-teeth light greenish-yellow, short, broad and blunt or even irregularly emarginate at apex; inner peristome darker, yellowish-brown in color, minutely roughened, columns supporting the dome (which would correspond to segments in normal peristome) slender, carinate without openings at keel; spores varying in size even in same capsule, up to $50\ \mu$, or more, the smaller ones of half this diameter or less, greenish-yellow, roughened, ripening in summer.

Of northern distribution, found in 3 localities in Michigan, occasional northward to Yukon and Alaska, Labrador and Greenland; also in Europe.

The following specimen was studied:

No. 21. University of Michigan Biological Station, Cheboygan, Michigan.
N = 14.

The gametophytic complement of 14 chromosomes (figs. 159–167) consists of 7 pairs. The average lengths of the 7 chromosome-pairs are as follows: $4.4\ \mu$, $3.9\ \mu$, $3.6\ \mu$, $3.3\ \mu$, $2.9\ \mu$, $2.5\ \mu$, $0.9\ \mu$. The chromosomes are about $0.3\ \mu$ wide. Two of the longer chromosomes have terminal spindle-attachment regions, the attachment regions of the very small chromosomes could not be determined. Other members of the complement have median or submedian attachment regions (figs. 166, 167).

DISCUSSION

The *Mniums* studied in this work can be separated into groups based on similarities of chromosome number and overall chromosome size, which with few exceptions parallel previous groupings based on morphological similarities alone. The basic chromosome number for the genus is 6. Chromosome size is not generally considered to be significant in considerations involving rather

distantly related organisms; however its importance in a small group of obviously closely related species cannot be ignored.

TABLE 1

SPECIES	CHROMOSOME		AVERAGE CHROMOSOME LENGTH IN MICRONS							
	NUMBER									
<i>Mnium Menziesii</i>	N = 5	7.4	6.6	5.6	5.2	4.6				
<i>Mnium stellare</i>	N = 7	12.1	10.6	10.0	9.9	7.0	6.3	1.8		
<i>Mnium hornum</i>	N = 6	5.7	5.5	5.2	5.0	4.5	4.0			
<i>Mnium orthorhynchum</i>	N = 6	7.2	6.7	6.3	5.8	5.5	5.0			
<i>Mnium marginatum*</i>	N = 12	7.3	6.4	6.0	5.6	5.2	4.7			
<i>Mnium spinulosum</i>	N = 8	6.8	6.6	5.8	5.4	4.8	4.2	2.6	2.1	
<i>Mnium Drummondii</i>	N = 6	5.9	5.4	5.2	5.2	4.9	4.5			
<i>Mnium cuspidatum*</i>	N = 12	6.4	5.6	5.2	4.8	4.4	4.1			
<i>Mnium cuspidatum</i>	N = 6	6.6	6.3	6.1	5.3	4.9	4.6			
<i>Mnium medium*</i>	N = 12	6.4	5.7	5.3	5.0	4.6	4.1			
<i>Mnium affine</i>	N = 6	6.5	6.0	5.6	5.2	4.8	4.3			
<i>Mnium affine</i> var. <i>ciliare</i>	N = 6	8.6	7.6	7.4	7.1	6.7	6.3			
<i>Mnium insigne</i>	N = 6	10.0	9.4	8.8	8.5	7.9	7.3			
<i>Mnium cinclidioides</i>	N = 6	10.3	7.6	7.2	6.5	5.8	5.2			
<i>Mnium punctatum</i>	N = 7	4.7	4.3	3.9	3.6	3.2	2.7	0.9		
<i>Mnium pseudopunctatum*</i>	N = 14	4.8	4.5	4.0	3.7	3.2	2.7	0.75		
<i>Mnium glabrescens</i>	N = 6	4.7	4.2	3.7	3.6	3.4	2.4			
<i>Cinclidium stygium*</i>	N = 14	4.4	3.9	3.6	3.3	2.9	2.5	0.9		

The following grouping was constructed using cytological data as the sole criterion.

- Group I.
 - Subgroup I.
 - Mnium hornum.* N = 6.
 - Subgroup II.
 - Mnium orthorhynchum.* N = 6.
 - Mnium marginatum.* N = 12.
 - Subgroup III.
 - Mnium spinulosum.* N = 8.
 - Subgroup IV.
 - Mnium stellare.* N = 7.
- Group II.
 - Subgroup I.
 - Mnium cuspidatum.* N = 6.
 - Mnium cuspidatum.* N = 12.
 - Mnium Drummondii.* N = 6.
 - Subgroup II.
 - Mnium affine.* N = 6.
 - Mnium medium.* N = 12.
 - Mnium affine* var. *ciliare.* N = 6.
 - Mnium insigne.* N = 6.
- Group III.
 - Mnium punctatum.* N = 7.
 - Mnium pseudopunctatum.* N = 14.
 - Mnium glabrescens.* N = 6.
- Group IV.
 - Mnium cinclidioides.* N = 6.

Kabiersch (1936) handled the above species in a similar manner in his critical division of the genus into sections and subsections.

* The average chromosome length for the diploids is given for chromosome-pairs.

The usual and convenient separation of the genus into three groups depending upon the marginal teeth of the leaves, i.e. single teeth, double teeth, and no teeth, is not so artificial as it would seem at first glance. The above species fall into these three groups as follows:

Double-teeth:

Mnium hornum.
Mnium orthorhynchum.
Mnium marginatum.
Mnium spinulosum.
Mnium stellare . . . ?

Single-teeth:

Mnium cuspidatum ($N = 6$).
Mnium cuspidatum.
Mnium Drummondii.

Mnium affine.

Mnium affine var. *ciliare.*

Mnium insigne.

Mnium medium.

Mnium cinclidioides . . . ?

No-teeth:

Mnium punctatum.

Mnium pseudopunctatum.

Mnium glabrescens.

The teeth of *Mnium stellare* are not always obviously of the double-toothed group. When well developed, however, they stand out at an angle to the plane of the leaf-blade and when close together give the appearance of double teeth.

The position of *Mnium cinclidioides* is questioned, since cytologically it is not similar to other members of the single-toothed group.

Disregarding the above two exceptions, the grouping is the same as that based on cytological evidence.

The cytological evidence separating the double-toothed from the single-toothed species is not too convincing. The basic chromosome number of 6 is the same in both groups. There is no consistent difference in chromosome size, with the exceptions of *Mnium cuspidatum*, *Mnium cuspidatum* ($N = 6$), and *Mnium Drummondii*. The chromosomes of these three are of the same size and noticeably smaller than other members of the two groups. The separation of the two groups cytologically is based upon the presence of subterminal or terminal spindle attachment regions in the double-toothed species and their absence in the single-toothed species.

The non-toothed group, as represented by the three species: *Mnium punctatum*, *Mnium pseudopunctatum*, and *Mnium glabrescens*, is more clearly natural. The chromosome size is the same for all three species and is much smaller than that of any other *Mnium* studied.

Some cytological evidence regarding the limits of the genus was obtained. *Mnium Menziesii* (see description) is a very distinct species with no apparent close relatives in the genus. Lindberg (1868) removed it from *Mnium* and proposed the name *Leucolepis acanthoneura* for it. Kabiersch (1936) agreed with Lindberg's conception, retaining the plant under the latter name. Andrews, in the *Moss flora of North America*, admits the distinct position of the plant but retains it in *Mnium*. The chromosome number is 5, in contrast to the basic number of 6 for the genus *Mnium* (figs. 1-10). The loss of a small chromosome fragment from a monoploid complement is known to have occurred in higher plants without causing the death of the cells involved but in most cases is accompanied by reduced vigor. However, the loss of a complete chromosome

from a monoploid complement, without lethal effects, is probably impossible. A reduction in chromosome number might possibly be effected by the translocation of all the material of one chromosome to other members of the complement with the exception of the spindle-attachment region which would then have to be eliminated (Sharp 1934). The above possible derivations of a 5-chromosome form from a basic number of 6 chromosomes are at best improbable, and especially when one considers the fact that to establish the new chromosome number in a dioicous plant such as *Mnium Menziesii* the event would have to occur simultaneously in plants of both sexes and the altered gametes would have to be brought together to produce a sporophyte which would then supposedly produce only spores having 5 chromosomes.

In view of the above difficulties in deriving the chromosome complement of *Mnium Menziesii* from some 6-chromosome form, it is more logical to suppose that the plant is not a *Mnium*, that it represents a different chromosome series, and should, following Lindberg, be maintained in the genus *Leucolepis*.

The similarity of *Cinclidium* (see description) to the non-toothed *Mniums*, *Mnium punctatum*, *Mnium pseudopunctatum*, and *Mnium glabrescens*, has been recognized as possibly indicating a close relationship. Loeske (1910), in fact, suggested the union of the above *Mniums* with *Cinclidium*. Morphologically, *Cinclidium* can be distinguished easily from *Mnium* only by peristome characters. The tissue of the inner peristome does not split to form teeth, as in *Mnium*, but remains united in a perforated, dome-like structure. The outer peristome-teeth, although similar to those in *Mnium*, are shorter. The gametophytic plants of *Cinclidium stygium*, the species studied in this paper, are essentially indistinguishable from those of *Mnium pseudopunctatum*. The chromosome number and chromosome morphology (figs. 159–167) suggest a very close relationship with *Mnium pseudopunctatum* (figs. 145–149). Both plants have 14 chromosomes, six relatively long pairs and a dimorphic pair of very short chromosomes. A comparison of chromosome lengths (table 1) between the two species, reveals a surprisingly close agreement and the chromosomes are also of the same width. Correlated with the apparently diploid condition of both species is the synoicousness of both. The chromosomes of *Mnium punctatum* ($N = 7$; figs. 133–144, table 1) agree very closely in length and width with the chromosome pairs found in *Cinclidium stygium*. The chromosomes of *Mnium glabrescens* also agree closely with those of *Cinclidium stygium* with the exception of the small seventh chromosome which is absent. Without doubt, *Mnium punctatum*, *Mnium pseudopunctatum*, and *Mnium glabrescens* are more closely related to *Cinclidium* than to other groups in the genus *Mnium*.

The suggestion that *Mnium cinclidioides* also shows the above affinities is not well supported cytologically. The chromosome lengths are quite different (figs. 111–120, table 1).

Whether the non-toothed *Mniums* should be united with *Cinclidium* is a

question to which the answer had best be delayed until more cytological data have been accumulated regarding other *Cinclidium* species, particularly those which are dioicous.

In many respects, *Rhizogonium spiniforme* reminds one very strongly of a double-toothed *Mnium*. The chromosome number is 6 (Kurita 1937, Lowry unpub.). However, the combination of 6 chromosomes and its synoicous inflorescence, a combination only found in *Mnium Drummondii*, coupled with its characteristic tropical distribution and peculiar growth habit, approaching the pleurocarpous type, makes a close relationship seem improbable. Unfortunately, data are lacking which would enable one to make a detailed comparison of chromosome morphology with *Mnium* species.

Five species belonging to the double-toothed *Mniums* were studied. *Mnium hornum*, *Mnium orthorhynchum*, *Mnium marginatum*, and *Mnium spinulosum* have well developed double teeth on the leaf margins, the teeth of *Mnium stellare* are not truly double but, as pointed out previously, are inserted at an angle to the plane of the leaf blade and when close together give the impression of double teeth.

The inclusion of *Mnium stellare* in the double-tooth group is done with considerable uncertainty, although its close morphological similarity to *Mnium Blyttii*, a plant which produces well developed double teeth, indicates that it does belong here. The chromosome number of *Mnium stellare* is 7, 6 long chromosomes with an "m" (figs. 11-21).

Heitz (1942) has found 7 chromosomes ($6 + m$) in *Mnium hymenophyllum*, a plant often found mixed with or confused with *Mnium Blyttii* (Andrews 1940), which suggests the possibility that a similar chromosome complement will be found for *Mnium Blyttii*. If such proves to be the case the position of *Mnium stellare* in the double-toothed group will be considerably strengthened.

Mnium stellare was placed in the non-toothed group by Limpricht (1893) and if one considers only the chromosome number, 6 with an "m," it apparently does belong there. A comparison of chromosome size between *Mnium stellare* (figs. 11-21) and *Mnium punctatum* (figs. 133-144) makes a possible relationship seem remote. The chromosomes of *Mnium stellare* are much larger.

The presence of the small seventh chromosome in *Mnium stellare* calls for some explanation of its origin, since the basic chromosome number for *Mnium* is clearly six. Fully aware that any explanation is necessarily hypothetical, the following possible origin is presented. If one chromosome with a subterminal attachment region, in an original complement of 6, broke through its attachment region, the result would be a relatively long chromosome and a very short chromosome. One would expect the two fragments to behave normally, since both would possess spindle attachment regions which would be located terminally. Such a chromosome fragmentation has been observed in *Zea* and the resulting fragments were found to behave as complete chromosomes (McClintock 1932, 1938). Since *Mnium stellare* is dioicous the fragmentation would have

to occur in plants of both sexes if the altered chromosome complement were to become established. The most logical point in the life history for the event to occur and involve both the chromosomes of both sexes simultaneously would be during the first meiotic division of the spore-mother cells. The almost complete sterility of the plant suggests an altered chromosome complement.

Mnium hornum, the type species of the genus, does not appear, cytologically, to be especially closely related to the other double-toothed species studied. The 6 chromosomes of *Mnium hornum* average 1 micron shorter than those of *Mnium orthorhynchum*. The plant is dioicous.

Mnium orthorhynchum and *Mnium marginatum* constitute a natural species-pair. The following gametophytic characters represent the only clearly defined differences between them. *Mnium orthorhynchum* is dioicous, there are on the average 2578 leaf-cells per square mm., and teeth are present on the back of the costa. *Mnium marginatum* is synoicous, there are on the average 2349 leaf-cells per square mm., and there are no teeth on the back of the costa. *Mnium orthorhynchum* ripens its spores in summer while those of *Mnium marginatum* ripen in May. The two plants have a nearly identical geographical distribution and are often found growing together, even mixed in the same clump. The chromosome numbers are as follows: *Mnium orthorhynchum*, $N = 6$, *Mnium marginatum*, $N = 12$ (figs. 25-36, 37-48). The twelve chromosomes of *Mnium marginatum* clearly represent 6 pairs (figs. 38, 44, 46). A comparison of the average chromosome lengths of *Mnium orthorhynchum* with the six chromosome-pairs of *Mnium marginatum* reveals no significant differences (table 1). *Mnium marginatum* is undoubtedly an autodiploid derived from *Mnium orthorhynchum*. The chromosome doubling must have been the result of apospory, regeneration of sporophytic tissue or the production of $2N$ spores, since doubling occurring in the gametophytic generation would not bring about the synoicous condition found in *Mnium marginatum*. It appears likely that the diploid does not represent an isolated instance of chromosome doubling, since the two species are often found mixed in a single collection.

Mnium spinulosum is aneuploid, $N = 8; 6 + 2$, with respect to the other species of the double-toothed group (figs. 49-60). The morphology of the species is distinctive and variable forms are not found (see description). An analysis of chromosome lengths reveals 6 chromosomes ranging in length from 6.8μ to 4.2μ , which is approximately the lengths found in the other species of the group. The two extra chromosomes are considerably shorter, 2.6μ and 2.1μ . Chromosomes of this size were not found in any of the other species studied. In formulating an hypothesis that would account for the origin of *Mnium spinulosum* it is necessary to postulate conditions which would bring about the synoicous character of the plant in addition to increasing the chromosome number from 6 to 8. The two extra chromosomes may have been derived, as was suggested for *Mnium stellare*, by fragmentation. The presence of terminal attachment regions (fig. 60), with the fact that chromosomes of a similar length to the two short chromosomes of *Mnium spinulosum* are not found in other

members of the genus, supports the fragmentation theory. Another interesting point is demonstrated by adding the two short chromosomes to the two next shortest chromosomes creating a hypothetical set of 6 and comparing with the complement of *Mnium orthorhynchum*.

Hypothetical complement	7.4	6.8	6.6	6.3	5.8	5.4
<i>Mnium orthorhynchum</i>	7.2	6.7	6.3	5.8	5.5	5

It is not suggested that *Mnium spinulosum* was derived from *Mnium orthorhynchum*. The above comparison merely points out that if *Mnium spinulosum* arose as the result of chromosome fragmentation, the original 6 chromosomes were possibly similar in length to those of the other members of the double-toothed group. The above mode of origin does not satisfy conditions necessary for the creation of the synoicousness of the plant. In the double-toothed group, 6 chromosomes and dioicousness are correlated, thus making it necessary to assume the synoicous character of *Mnium spinulosum* to be the result of genetic change. The synoicousness of *Mnium spinulosum* is more easily explained if the aneuploid were the result of irregular meiotic divisions following hybridization between a dioicous, 6-chromosome form and a synoicous, 12-chromosome form.

Five species and one variety representing the single-toothed group were studied. The basic gametophytic chromosome number is 6. There is considerable variation in chromosome size within the group; *Mnium cuspidatum*, *Mnium cuspidatum* ($N = 6$), and *Mnium Drummondii* form one size group with chromosomes somewhat shorter and thinner than the other species. A progressive increase in chromosome size is found in *Mnium affine*, *Mnium affine* var. *ciliare*, and *Mnium insigne*.

Mnium cuspidatum ($N = 12$; figs. 67–78) is an autodiploid. Here again the synoicous inflorescence is correlated with a $2N$ chromosome complement. The chromosomes consist of 6 pairs, the members of each pair being of equal length. If *Mnium cuspidatum* is an autodiploid, one would expect to find a haploid, dioicous moss similar to *Mnium cuspidatum*. Such a plant is represented by collection No. 13 which is referred to in this work as *Mnium cuspidatum* ($N = 6$). The 6-chromosome form is somewhat smaller than the species and the leaf-cell size is smaller, having 2881 cells per square mm. as compared to 1885 cells per square mm. The form was sterile and the sex condition could not be determined; presumably it is dioicous. The chromosome number is 6 (figs. 79–86). The average lengths of the chromosomes agree reasonably well with those of the 6 chromosome-pairs of *Mnium cuspidatum*. The two forms are obviously very closely related since *Mnium cuspidatum* is the aposporous autodiploid of the form.

Mnium Drummondii is a distinct and stable species easily distinguished from all other Mniums. In morphological characters it approaches *Mnium cuspidatum* more closely than any of the other members of the genus. It differs from the above species in leaf-cell size, 800 cells per square mm. as compared to

1885 cells per square mm. of *Mnium cuspidatum*, the regular hexagonal shape of the cells, the tendency to produce several sporophytes from the same inflorescence, and its restricted geographical distribution (see description). The plants are normally synoicous but occasional male plants are found of the characteristic *Mnium* type, having broad, terminal rosette of perigonal leaves, and clavate paraphyses. The chromosome number is 6 (figs. 61–66), which is surprising since all other members of the genus having 6 chromosomes are dioicous. One is thus forced to consider the possibility that *Mnium Drummondii* may be diploid, having evolved from a 3-chromosome dioicous form. The work of the Marchals, Wettstein and others (see introduction) has shown that recently-produced diploids of dioicous species develop many plants which are apparently unisexual and only a small proportion of synoicous plants. Perhaps the occasional production of a typically male inflorescence by *Mnium Drummondii* is an expression of instability resulting from a not-too-remote chromosome doubling. Allowing for errors in measurements, the 6 chromosomes of *Mnium Drummondii* may be grouped into 3 pairs (table 1). In speculations of this type, one must not overlook the possibility of changes in the germ plasm without accompanying visible alterations in the chromosomes, which would be capable of altering the mechanism governing sex expression.

Mnium affine (see description) and *Mnium medium* (see description) form a natural, closely-related species-pair. There are only two morphological characters which will infallibly separate them, namely leaf-cell size and sex condition. The leaf cells of *Mnium medium* are larger, 575 cells per square mm., than those of *Mnium affine* which has 615 cells per square mm. *Mnium medium* is synoicous and *Mnium affine* is dioicous. *Mnium affine* has 6 chromosomes (figs. 121–132) and *Mnium medium* is diploid with 12 (figs. 87–98). The 6 chromosome-pairs of *Mnium medium* agree closely in length with the 6 chromosomes of *Mnium affine* (table 1). Here, as in the other species-pairs of the genus, *Mnium medium* is apparently an autodiploid derived from *Mnium affine* by some type of apospory.

Mnium affine is variable in the character of the leaf-margin teeth. There are forms in which teeth are much reduced to nearly absent and at the other extreme, forms having long, sharp teeth consisting of several cells. The latter form is represented by specimen No. 9 and is here referred to as *Mnium affine* var. *ciliare* (Grev.) C. Müll. The chromosome number is 6 (figs. 130–132). The chromosomes are larger than those of the species and remind one of the chromosomes of *Mnium insigne* (figs. 99–110). Andrews (1940) says, "*Mnium insigne* is obviously a derivative of the widely distributed and greatly varying *Mnium affine*." A detailed comparison, in so far as data permit, of the chromosomes, suggests such a relationship. Both species have 6 large chromosomes, those of *Mnium insigne* are next to the largest found in the genus. Subtracting the average lengths of the chromosomes of *Mnium affine* var. *ciliare* from those of *Mnium insigne* yields the following results: 1.4 μ , 1.8 μ , 1.4 μ , 1.4 μ , 1.2 μ , 1 μ . There are no great differences in relative lengths, although the chromo-

somes of *Mnium insigne* are longer. A comparison of spindle attachment regions of the two chromosome sets reveals no great differences. All are submedian or median (figs. 132, 108).

Mnium cinclidioides (see description), although superficially resembling *Cinclidium*, does not show cytological affinities in the direction of this genus or toward the non-toothed *Mniums*. It is best treated as a separate section of the genus, without close relatives, as was done by Kabiersch. The gametophytic chromosome number is 6. The chromosomes are long and quite thin, which gives the complement a characteristic appearance not found elsewhere in *Mnium* (figs. 111–120). One chromosome is noticeably longer, 2.7 μ , than the others (table 1) and can be designated as an "M" chromosome. The shortest chromosome of *Mnium cinclidioides* is longer than the longest chromosome found in either the non-toothed *Mniums* or in *Cinclidium*.

The non-toothed *Mniums*, represented by Andrews' description as *Mnium punctatum*, are characterized cytologically by the small size of their chromosomes. The largest chromosome is only 4.8 μ by 0.3 μ . In Andrews' treatment in the *Moss flora of North America* all forms are included in *Mnium punctatum*, with the statement, "Variable in many of its features. Of the different characters that have been employed to separate *Mnium pseudopunctatum* (*M. subglobosum*) none, even its synoicous inflorescence, appears to correlate with any others and it seems impossible to distinguish under this name even a clearly marked variety." Of the Pacific Coast form, Andrews states, "*M. glabrescens* Kindb. has often been regarded as a valid species of the Pacific coastal region and may give somewhat that impression, but presents no characters that definitely separate it. Its leaf cells average smaller than usual, but vary greatly even in the same leaf." Three collections of *Mnium punctatum* were studied cytologically: Collection No. 2 from Michigan, a dioicous, rather small form corresponding closely to the description of *Mnium punctatum*; No. 17, also from Michigan, a synoicous form referable to *Mnium pseudopunctatum*; and No. 20 from Oregon, a dioicous form representing *Mnium glabrescens*. One finds a basis for separating definitely the above species in their chromosome numbers which are, respectively, 7, 14, and 6 (figs. 133–144, 145–149, 150–158). The chromosome complement of *Mnium punctatum* is made up of 6 long chromosomes plus one very short "m" chromosome (table 1). The "m" chromosome has been identified in European material by Jachimsky (1935), as a sex-chromosome.

The synoicous *Mnium pseudopunctatum* is apparently an autodiploid derivative of *Mnium punctatum* (figs. 145–149). Of the 7 chromosome-pairs, one of them consists of two "m" chromosomes, presumably the x and y sex-chromosomes of *Mnium punctatum*. A detailed comparison of average chromosome lengths reveals a maximum difference of only 0.2 μ between the two species (table 1). In addition to 14 chromosomes and synoicousness, *Mnium pseudopunctatum* presents other diploid characteristics differentiating it from *Mnium punctatum*. The leaf cells are larger, a character which is difficult to

measure, because of the variable size of the cells in different parts of the leaf; however, by carefully selecting the same relative position in each leaf examined, the following reasonably constant results were obtained: *Mnium punctatum*, 465 cells per square mm.; *Mnium pseudopunctatum*, 390 cells per square mm. The rhizoids which cover the lower part of the stem show a different mode of branching in the two species, dichotomously with short internodes in *Mnium pseudopunctatum*, deliquescent with relatively long internodes in *Mnium punctatum*. This character does not seem to be the result of different environmental factors, since the characteristic branching was maintained by the two plants when grown side by side in the same damp chamber.

Heitz (1942) found only 13 ($12 + m$) chromosomes in the European *Mnium pseudopunctatum* and suggested hybridization between *Mnium punctatum* and some unknown 6-chromosome form as its origin. *Mnium glabrescens* (figs. 150–158) is such a form with 6 chromosomes. The plant is quite similar to *Mnium punctatum* except for the more narrowly oval leaves, slightly smaller leaf cells, 480 per square mm., and its very restricted geographical distribution. The 6 chromosomes are of nearly the same length as the 6 long chromosomes of *Mnium punctatum* (table 1). The above morphological differences, correlated with the chromosome number of 6, are here considered sufficient justification for considering *Mnium glabrescens* a distinct species. The basic chromosome number for *Mnium punctatum* and *Mnium pseudopunctatum* is undoubtedly 6, the "m" chromosome having probably arisen as the result of fragmentation. In figure 149, there are indications of terminal spindle-attachment regions in two of the longer chromosomes, which is the result expected if fragmentation had occurred through this structure.

In general, the cytological data obtained in this work support the concepts of the morphological taxonomist, and in the matter of polyploids imposes a somewhat narrower interpretation upon the separation of species. It has been customary to regard experimentally produced, semi-sterile, diploid forms as varieties, and rightly so, for one of the obvious requirements of a good species is that it must be able to maintain itself in nature. *Bryum Corrensii* was not given specific rank until the plant had established complete fertility. Most naturally occurring polyploids have been given specific rank, although Andrews does not recognize *Mnium pseudopunctatum*. In this connection it is interesting to note the status of the haploid form of *Mnium cuspidatum*. To be consistent with the treatment of *Mnium medium* and *Mnium marginatum*, the form should be given specific status.

Autopolyploidy, although not ordinarily considered as important in the evolutionary process leading to species production as allopolyploidy, does produce changes of a specific nature in the dioicous mosses, for example synoicousness and increased cell size. The "gigas" characters may be lost eventually, as in *Bryum Corrensii*, and there is not always a perfect correlation between cell size and chromosome number. A maximum cell size may be reached in which further increase in chromosome number does not result in further increase in

cell size (Wettstein 1924c, 1928b). In spite of the above exceptions, however, the synoicous character of the inflorescence effectively isolates the autopolyploid moss from its haploid progenitor by making self-fertilization practically certain.

The cytological evidence obtained in my work is necessarily an indirect indication of relationships and the need for experimental corroboration is obvious if such conclusions as have been made are to be removed from the status of hypotheses. Aposporic diploids of the haploid members of the species-pairs should be produced artificially and compared with the natural diploids. The matter of sex determination needs further investigation. Single-spore cultures of each species should be made to determine the true sex condition positively. Many of the *Mniums* are described as dioicous merely because the antheridia and archegonia are produced on different leafy plants with no assurance that the plants originated from different spores. The European *Mnium hornum* was examined by the Marchals and found to be really dioicous. However, the variable, synoicous to heteroicous nature of *Mnium Drummondii* throws suspicion upon other 6-chromosome, supposedly dioicous species. The synoicousness of the hyperploid *Mnium spinulosum* also emphasizes the need for a more thorough knowledge of the subject.

The presence of the "m" chromosome in *Mnium stellare* and *Mnium punctatum* suggests the possibility of producing chromosome fragmentation through the use of X-rays or other physical means. It would be particularly interesting to irradiate *Mnium glabrescens* ($N = 6$), in order to validate the supposition that one of the chromosomes has a tendency to break through its spindle attachment region, forming a 7-chromosome complement like that of *Mnium punctatum*.

SUMMARY

1. Cytological researches on mosses are reviewed, with special emphasis on chromosome numbers and polyploidy, and a list of published reports of chromosome numbers in mosses is given.

2. The genus *Mnium* was selected because of the availability in Michigan of more than half of the 21 North American species.

3. Special techniques to investigate and count chromosomes of mosses were devised, consisting especially of a smear technique for the apex of the gametophyte plant.

4. Fixation was made with a 1:2 solution of acetic acid and absolute alcohol; staining was accomplished by means of acetic orcein.

5. Fifteen species of *Mnium* are described on the basis of their external morphology, which is correlated with their chromosome morphology.

6. The chromosome number and morphology of 15 North American species of *Mnium* and of *Cinclidium stygium* were determined.

7. The basic chromosome number for the genus *Mnium* is 6.

8. It is suggested that *Mnium Menziesii* be excluded from the genus *Mnium*

and retained in the genus *Leucolepis* Lindb. on the basis of its 5 chromosomes, coupled with morphological differences.

9. Three aneuploid species were found, *Mnium stellare*, $N = 7$, *Mnium spinulosum*, $N = 8$, and *Mnium punctatum*, $N = 7$. It is postulated that the extra chromosomes arose as the result of fragmentation.

10. The average chromosome lengths for 15 species, 1 variety and 1 form of *Mnium* and for *Cinclidium stygium* were determined.

11. It was concluded that the cytological data indicate a relationship between *Cinclidium* and the non-toothed *Mniums*, represented by *Mnium punctatum* and *Mnium pseudopunctatum*, that is closer than between the latter species and other *Mniums*.

12. Four species-pairs are recognized:

<i>Mnium orthorhynchum</i>	$N = 6$	<i>Mnium marginatum</i>	$N = 12$
<i>Mnium cuspidatum</i>	$N = 6$	<i>Mnium cuspidatum</i>	$N = 12$
<i>Mnium affine</i>	$N = 6$	<i>Mnium medium</i>	$N = 12$
<i>Mnium punctatum</i>	$N = 7$	<i>Mnium pseudopunctatum</i>	$N = 14$

It was concluded that the diploid members of the above species-pairs are aposporic autodiploids of the haploid members.

13. *Mnium Drummondii* was found to possess 6 chromosomes and a synoious inflorescence, a condition not found in other 6-chromosome *Mniums*. The occasional production of a male inflorescence by this species is interpreted as possibly indicating an unstable condition as the result of a recent, aposporic chromosome doubling of some unknown dioicous, 3-chromosome form. It was pointed out that the 6 chromosomes of *Mnium Drummondii* may be grouped into 3 pairs, the members of each pair being of similar length.

14. Similar chromosome size and spindle-attachment regions of *Mnium affine* var. *ciliare* and *Mnium insigne* are interpreted as supporting evidence to the previously postulated close relationship between these two species.

15. *Mnium cinclidioides* is placed in an independent position on the basis of its unique external morphology and chromosome morphology.

16. The 6-chromosome complement of *Mnium glabrescens*, in contrast to the 7-chromosome complement of *Mnium punctatum*, is considered as sufficient additional evidence for retaining the plant as a good and independent species.

17. It is suggested that the haploid form of *Mnium cuspidatum*, to be consistent, should be given specific rank, since it maintains itself in nature.

18. The synoious inflorescence was found to be correlated with the diploid gametophyte in all species studied with the exceptions of *Mnium Drummondii*, apparently haploid ($N = 6$) and *Mnium spinulosum*, hyperhaploid ($N = 8$).

19. The cytological data support the concepts already proposed by morphological taxonomists, and a classification based on cytological interrelationships is proposed.

20. Autopolyploidy is considered to be more important than allopolyploidy in species production in *Mnium*.

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